Studies on Neotropical Pseudophyllinae: Integrative description of *Dentotibium* gen. nov., and of a toothed foretibia katydid (Orthoptera: Tettigoniidae) that sings from burrows in branches

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Abstract

Herein, we describe the genus *Dentotibium* **gen. nov.** and the species *D. ramucantoris* **sp. nov**, a toothed foretibia katydid within the subfamily Pseudophyllinae from Colombia. This new katydid is a forest dweller inhabiting oak woodlands between 1600 and 2300 m above sea level, only found in the western slopes of the Eastern Andes of Boyacá Department, Colombia. This new species burrows in woody branches and shows big heads in both sexes. The appearance of *Dentotibium* **gen. nov.** is similar to that of *Trichotettix* Stål, 1873 but differs in having tubercles over the dorsal margin of the foretibiae. It is also close to *Nastonotus* Bolívar, 1890, but differs from in lacking the three black stripes in the vertex and having a less marked frontal suture and smoother face. Males sing all night long, and their calling song consists of periodic syllables with three differentiable phases. Seasonal calling activity lowers remarkably during the dry season (Jun–Aug). DNA barcoding sequences for the paratypes made available in a previous study are included here.

Keywords

Introduction

The diversity of sylvan katydids (Pseudophyllinae) in the Neotropics is astonishing, only surpassed by Phaneropterinae as evidenced in the few studies on Amazonian katydids available (Nickle and Castner 1995). Although this subfamily currently includes more than 1000 species and 240 genera globally (Cigliano et al. 2023), the taxonomic knowledge of this group is still incipient, with many groups yet to be described. This is the case even in well-studied areas such as Panama and Costa Rica (Nickle 1992, Naskrecki 2000). In addition, there are evident gaps in other areas of the Neotropics, such as the Andean region (Chamorro-Rengifo et al. 2011, Cadena-Castañeda et al. 2016, 2020, Cadena-Castañeda and Garcia Garcia 2017).

As scarce as the studies on species diversity of ensiferans are, other kinds of studies in acoustic, ecological, and genetic diversity are even more so (Morris and Beier 1982, Morris et al. 1989, Nickle 1992, Montealegre-Z and Morris 1999, Naskrecki 2000, Cadena-Castañeda and Páez 2013, Heller et al. 2015, Mugleston et al. 2018, Benavides-Lopez et al. 2020, Cadena-Castañeda et al. 2022a). Very few examples of bioacoustics and emission strategies have been presented for the already described species, including a broad range of frequencies and signaling alternatives that allow tettigonids to communicate by overcoming barriers that block the signals (Robinson and Hall 2002, Montealegre-Z 2009, ter Hofstede et al. 2020, Cadena-Castañeda et al. 2022b).

One of the most diverse groups of Neotropical pseudophyllines are those of the tribe Cocconotini, a phenotypically diverse group (Beier 1960, 1962, Kevan 1989, Cadena-Castañeda et al. 2020). Most species are macropterous, and a few are brachypterous. Several species of the latter prefer highlands, such as paramos, high Andean forests, and cloud forest habitats (Cadena-Castañeda et al. 2022b). There are very few bioacoustic studies on Colombian short-winged Cocconotini, including works on *Trichotettix pilosula* Stål, 1873 (Montealegre-Z and Morris 1999, Morris and Montealegre-Z 2001) and *Nastonotus foreli* Carl, 1921 (Baker et al. 2019). This panorama demonstrates that there is still pending work in this discipline for many taxa of the Colombian pseudophyllines.

In addition to providing basic morphological taxonomy, we wish to highlight the importance of adopting integrative taxonomic approaches by including additional sources of taxonomic information, such as bioacoustics descriptions and DNA sequencing, in order to facilitate future comparative analysis or to inform future conservation programs (Pante et al. 2015). Here, we describe

a new genus and species of a foretibia-toothed Cocconotini that sing from burrows in branches and lianas from the Colombian Eastern Andes. Given the particular behavior of this new taxa, we also describe its bioacoustics and provide natural history information regarding the acoustic diel activity of the species. In addition, we highlight the DNA barcoding of the new taxa paratypes previously done by Baena-Bejarano et al. (2023). This is the continuation of previous contributions to the study of pseudophyllines, led by the first author of this paper (Cadena-Castañeda 2011, Cadena-Castañeda and Braun 2011, Cadena-Castañeda and Monzón-Sierra 2014, Cadena-Castañeda et al. 2016, 2020, 2021, 2022b,c).

Materials and methods

Study sites.—We found the new genus and species in two different sites. The first site was in Coper, Vereda Turtur, Sector San Ignacio (Boyacá Department), at an elevation of 1600 m. Coper belongs to the western province of the Boyacá Department and is located 133 km from Tunja, the capital city of Boyaca. Elevation ranges from 600 to 2600 m above sea level. The average temperature is 23.8°C, and the annual precipitation is 3152 mm. Within the elevation range, the area sampled in Coper was 202 km² and included three different thermal floors: warm, 171 km²; temperate, 17 km²; and cold, 14 km².

We also explored the "Reserva Natural y Cascada Los Tucanes" (RNCLT; previously known as "Los Yátaros"). This private reserve of 16 ha of sub-Andean and oak forests is under different regeneration statuses. Its elevation ranges from 2100 to 2300 m, and the average temperature is 15°C. The annual media precipitation of the reserve is 1450 mm, with two rainy periods: from March to May and from October to November (Secretaría de Salud de Boyacá 2013). It is located 6 km from Gachantivá town, department of Boyacá, Eastern Andes of Colombia.

Genital preparations.—We followed Cadena-Castañeda (2015) for the dissection of genitalia. The genital terminology follows Chamorro-Rengifo and Lopes-Andrade (2014): ejaculatory duct (**ejd**), ejaculatory vesicles (**ejv**), dorsal lobe (**dl**), dorsal fold of dorsal lobe (**ddl**), lateral folds of dorsal lobe (**ldl**), lower folds of ventral lobe (**lw.vl**), titillators (**ti**), and upper folds of ventral lobe (**up.vl**).

Photographic procedure.—Lateral and dorsal view photographs were captured using a D3400 digital camera, while a Carl Zeiss Stemi 305 trino stereomicroscope was used to capture the remaining morphological characters.

Measurements and venation nomenclature.—Measurements, in mm, are defined as follows: *length of body* (**LB**), distance from the frons to the abdominal apex, excluding ovipositor or wings; *dorsal length of pronotum* (**Pr**), maximum distance between the anterior and posterior pronotal margins; *length of tegmina* (**Teg**), from base to apex; *length of hind femur* (**HF**), from the base to the genicular lobes; *length of hind tibia* (**HT**), from the genicular lobe to apex; *length of subgenital plate* (**SP**), distance from its base to its apex; *length of ovipositor* (**Ov**) from the base to the dorsal valve to the apex. The venation nomenclature follows Desutter-Grandcolas et al. (2017).

Collections.—The studied specimens are deposited in the Colección de Artrópodos y otros Invertebrados at the Universidad Distrital Francisco José de Caldas, Bogotá, Colombia (CAUD) and the Colección de Entomología at the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia (IAVH-E).

Acoustic recordings and analysis.—In the RNCLT, we located individuals inside the oak forest through active search, and we captured them by taking the piece of branch in which we found the burrow. For recording in captivity, a piece of the vine of about 50 cm alongside the specimen was kept in a metal mesh cage, with dog food and water given *ad libitum*. We recorded the calling song from two males different from the holotype and paratypes (yet to be deposited in the entomological collection). The first one (specimen A) was recorded with a Dodotronic® Ultramic 192K EVO set to a sampling rate of 192 kHz and a 16-bit resolution; this included use of a directional cone accessory at 21.6°C, 50% relative humidity, and 150 cm from the caged individual in a controlled closed space. The second one (specimen B) was recorded with the integrated microphone of an AudioMoth (1.0.1.) recorder set to a sampling rate of 384 kHz and a 16-bit resolution at a temperature of 13.7°C, 85% relative humidity, and 50 cm from a caged individual in an open area close to the original habitat. Both microphones were located facing the burrow entrance. The original recording for specimen B was deposited in the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt's Colección de Sonidos Ambientales Mauricio Álvarez Rebolledo soundscape collection with catalog number IAvH-CSA-18787. Relative humidity and temperature measurements were taken using a RadioShack® 11A12 wired thermometer.

We quantified acoustic parameters for the two individuals following Baker and Chesmore's (2020) terminology for the following calling song parameters: pulses, pulse duration, pulse period, pulse peak frequency and pulse -10 dB bandwidth, syllables, syllable duration, syllable period, syllable peak frequency, and syllable -10 dB bandwidth. Three additional terms were defined and included that we felt would be particularly useful for comparing the species' calling song with future new species in the genus: these are the syllable sections (see results), -10 dB bandwidth lower limit and -10 dB bandwidth upper limit. The species calling song includes harmonic peaks, which were not measured. Measurements were made using ocenaudio 3.13.4 (FFT length 512, Hamming window, 90% overlap; Ocenaudio Development Team, 2024). Sample spectrograms and oscillograms were generated using the packages *seewave* and *ggplot* (FFT length 512, Hamming window, 90% overlap) in R (Sueur et al. 2008, Wickham 2016), with a maximum plotted frequency of 100 kHz. The single call in Fig. 6 was plotted up to 40 kHz.

To estimate the daily and annual acoustic activity of the *Dentotibium ramucantoris* **gen. nov.** et **sp. nov.**, we used a passive acoustic sampling dataset conducted in RNCLT (Tovar-Garcia and Acevedo-Charry 2021). This dataset comprised one-minute recordings made each 30 minutes throughout the day for 40 weeks, from March 1, 2020 to January 22, 2021; this allowed us to extract the number of specific acoustic detections per hour of each day at a single site in RNCLT (Gomez-Morales and Acevedo-Charry 2022). The monitoring was not continuous due to the COVID-19 lockdown restrictions during February and September, May and June (gaps in weeks 5–8, 19–23, and 36–39; Fig. 8). We used the same spectrogram pattern-matching model with the audible section of the acoustic signal (13–24 kHz) from Gómez-Morales and Acevedo-Charry (2022) within the ARBIMON platform (Aide et al. 2013), available from Rainforest Connection (https://arbimon.rfcx.org/). The pattern-matching model ran over 11882 recordings, detecting the species in 23% of the recording dataset. For details on the model training, accuracy, and performance, refer to "Katydid 5" in Gómez-Morales and Acevedo-Charry (2022).

Results

<div align="center">

Order Orthoptera Olivier, 1789
Suborder Ensifera Chopard, 1921
Superfamily Tettigonioidea Krauss, 1902
Family Tettigoniidae Krauss, 1902
Subfamily Pseudophyllinae Burmeister, 1838
Tribe Cocconotini Brunner von Wattenwyl, 1895

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Dentotibium Cadena-Castañeda & Gomez-Morales, gen. nov.

https://zoobank.org/720B57AC-F2AA-4986-BBAD-6343DE85A502

Type species.—*Dentotibium ramucantoris* **gen. nov.** et **sp. nov.** by original designation and monotypy.

Generic diagnosis and comparison.—*Dentotibium* **gen. nov.** is close to *Nastonotus* Bolívar, 1890, as both genera are brachypterous and have tubercles over the dorsal margins of the foretibiae. Nevertheless, *Nastonotus* differs from *Dentotibium* **gen. nov.** by its fronto-genal suture being very marked and its face being very rugose, unlike the latter, which has the whole head smooth and lacks sutures that delimit the face from the rest of the cephalic capsule. Furthermore, *Nastonotus* species have three black stripes on the vertex, the main one going over the medium line of the pronotum, while *Dentotibium* **gen. nov.** lacks these lines. The tenth tergite in *Nastonotus* is elongated, and the cerci are distally elongated, very slim, sclerotized, and acuminate. The new genus has only the preapical ventral spine, which is robust and hook-shaped.

Trichotettix Stål, 1873 is also similar to the new genus but differs in morphology. The surface of the pronotum and legs of *Trichotettix* is densely covered by thick hairs, while *Dentotibium* **gen. nov.** has few and thin hairs. *Trichotettix* does not have ventral spines on the fore and middle femora or the dorsal tubercles of the foretibia, both of which occur in the new genus. The cerci of *Trichotettix* males are thin and armed with two sclerotized spines of similar size, while *Dentotibium* **gen. nov.** has only one preapical spine curving downward. As for the internal genitalia, the **ti** of *Trichotettix* is well-sclerotized in a peduncular structure, while the **ti** of the new genus is membranous and barely differentiates itself from the rest of the genital structures. *Trichotettix* females have a wide ovipositor, and the last sternite does not have modifications or folds, as occurs in *Dentotibium* **gen. nov.**

Other brachypteran Cocconotini genera that resemble *Dentotibium* **gen. nov.** include *Nannotettix* Redtenbacher, 1895, and *Natagaima* Beier, 1960, which are also distributed on the eastern slope of the Colombian Andes Mountain range and its inter-Andean valleys. These genera differ from *Dentotibium* **gen. nov.** in that they are more slender and are a reddish-brown or ocher color; both genera have a black midline that crosses the pronotal disc. *Nannotettix* and *Natagaima* do not have dorsal denticulations of the foretibia. The last sternite of the females is not modified, and the ovipositor is also more slender as well, in contrast to females of the new genus.

Dentotibium **gen. nov.** also resembles the genus *Gnathoclita* Haan, 1843, of the tribe Eucocconotini, particularly the brachypteran species. The main differences between both genera are the same as those between the new genus and *Trichotettix* (except for the hairs on the pronotum and legs and the shape of the cerci, which are unique to *Trichotettix*). The most notable difference is the modification and lengthening of the mandibles of *Gnathoclita males* projecting forward, which does not happen in the new genus.

Etymology.—The name of the genus derives from the conjunction of the Latin "*dento*" and "tibium" in reference to the teeth present on the dorsal margin of foretibiae. The gender of this name is being established as neuter.

Description.—Mid-sized (body length 21–36 mm) and moderately robust body (Figs 1, 4). Coloration. Body coloration predominately ocher, with black stripes in head and pronotum; tegmina black with yellow veins (Figs 1, 4). Head. Globose (Fig. 1A, B), space between antennal sockets as wide as half of width of antennal scape; fastigium slightly raised, narrow, and with ocelli located on each side (Fig. 1C); rugose cephalic capsule surface; scape and pedicel without spines; maxillary palpi moderately elongated (Fig. 1D); mandibulae symmetric and with similar development in both sexes. Thorax. Pronotum granulose (Fig. 1A, D), anterior border curved and projected forwards; sulci divide the deep and present zones of the pronotum (Fig. 1B); lateral lobes of pronotum quadrangular, humeral sinus not developed (Fig. 1D). Sternum. Prosternum armate, with two little conical spines; mesosternum and metasternum wider than long, with rounded lateral lobes lacking spines or tubercles not making contact over ventral margin; mesofurcal groove narrow with the two holes close to each other. Wings. Brachypterus, fore and hind wings covering near the half of the abdomen (Figs 1, 2A–E). Legs. Moderately robust, with two or three spines on the ventral side of the fore and mid femur, less when compared to other genera of the tribe. Fore coxae armate, with a conspicuous dorsal spine (Fig. 1D); all the coxae ventrally unarmed. Foretibia armate dorsally, with two rows of tubercles, each one over each dorsal border from the tympanum to the apex (Fig. 1C, D). Abdomen cylindrical (Fig. 2F–H), tenth tergite and epiproct without modification in males (Fig. 2F, G) and females (Fig. 5D); male cerci robust and armed with a preapical spine (Fig. 2F). Male subgenital plate almost as long as wide and with articulate styli (Fig. 2H). Female's last abdominal sternite modified, with folds in the apex (Fig. 5F, G). Ovipositor robust, almost as long as the hind femur (Fig. 5D, E). Female subgenital plate without modifications (Fig. 5G). **Male genitalia.** Predominantly membranous, ti moderately sclerotized over the posterior margin, vdl differentiated and wavy in the apex (Fig. 3).

Distribution.—Mid and highlands of Boyacá, Colombia, between 1600 and 2300 m above sea level.

Comments.—This new genus can be easily confused with *Trichotettix*, especially due to the coloration of the type specimen of *Trichotettix pilosula* Stål, 1873, which has a color pattern similar to that of *D. ramucantoris* **gen. nov.** et **sp. nov.** However, the specimens of *T. pilosula* studied by Montealegre-Z and Morris (1999) have a reddish-brown color but fit the morphology of the type specimen studied by the authors. The most likely reason for this color difference is that the type specimen, preserved in alcohol, lost its original coloration. It is common for reddish specimens preserved in alcohol for a long time to turn into various shades of ocher. In contrast, the ocher coloration of the studied specimens of *D. ramucantoris* **gen. nov.** et **sp. nov.** was preserved by keeping the specimens alive until description and, subsequently, in dry conservation in entomological collections.

Trichotettix nuda Beier, 1960 was originally described based on a subadult female that was eventually found to correspond to an undescribed genus from the paramos surrounding Bogotá city (Colombia's capital). For this reason, *T. nuda* is not considered to belong to *Trichotettix* and will be reassigned outside of Cocconotini in a forthcoming description of the new genus and the adult stages (Cadena-Castañeda in prep.). Thus, we rule out this species as being related to *D. ramucantoris* **gen. nov.** et **sp. nov.**

Dentotibium ramucantoris
Cadena-Castañeda & Gomez-Morales, sp. nov.
https://zoobank.org/F00D7892-70AF-43AB-AEB7-9A48FF5B0C3D
Figs 1–6

Etymology.—The species name derives from the conjunction of the Latin *"ramus"* (*"branch"*) and *"cantor"* (*"singer"*), referencing how this new species sings from inside the burrows of branches and lianas. The specific epithet is substantive and independent of grammatical gender.

Type material.—**Holotype—**COLOMBIA • ♂; Boyacá, Coper, Vereda Turtur, Sector San Ignacio; 1600 m.; 5°25'32.03"N, 74°0'15.24"W.; October 2019.: O.J. Cadena-Castañeda leg.; CAUD.

Paratypes—COLOMBIA • 2♂, 2♀; same data as holotype; CAUD • 2♂; Boyacá, Gachantiva, Vereda la Caja, Reserva Natural y Cascada Los Tucanes, 2100–2300 m; 5°47'21.336"N, 73°33'1.584"W; September 2020; Diego A. Gomez-Morales leg (IAVH-E218714); September 2020; Diego A. Gomez-Morales (IAvH-E218391); CAUD • 1♂; Boyacá, Gachantiva, Vereda la Caja, Reserva Natural y Cascada Los Tucanes; 2100–2300 m; 5°47'21.336"N, 73°33'1.584"W; 23 January 2021; Diego A. Gomez-Morales leg.; CAUD.

Description.—**Male.** In addition to the characters mentioned above: *Coloration.* Ochre-colored head, thorax, and legs; light brown abdomen (Fig. 1). Head with a black stripe from inferior border of antennal sockets, surrounding eye sockets, and reconnecting dorsally, covering the fastigium (Fig. 1C); eyes light purple; mandibles dark
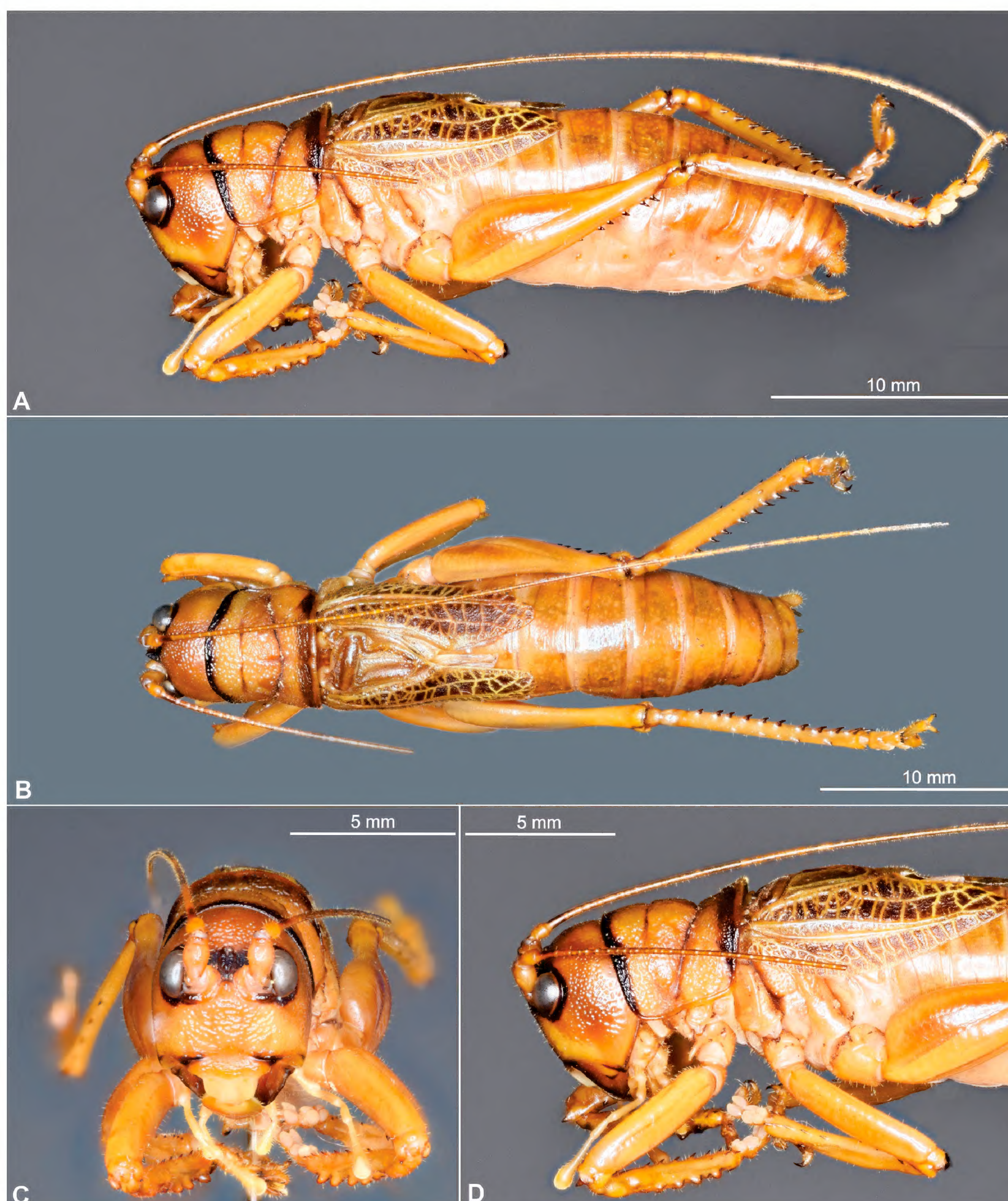

Fig. 1. *Dentotibium ramucantoris* **gen. nov. et sp. nov. Male. A.** Habitus in lateral and **B.** dorsal views. **C.** Frons. **D.** Head and thorax in lateral view.

reddish brown with black internal borders (Fig. 1C, D); pronotum with black delineated sulcus on anterior and posterior margins (Fig. 1B, D); femora apex, foretibia dorsal margin, and foretibia base blurred in reddish brown; tegmina black and with yellow venation (Fig. 2A–D), hind wings translucid; tenth tergite with two ovoid light brown spots, one on each side (Fig. 2G). *Head.* Big, pedicel

with a basal tubercle on the ventral margin; fastigium small and elevated (Fig. 1C), triangular in dorsal view (Fig. 1B), with small and rounded ocelli on each side; frontal ocelli inconspicuous (Fig. 1C); first, second, and third segments of maxillary palpi of similar size; fifth segment longer and dilatates toward the apex (Fig. 1D). *Thorax.* Anterior margin of pronotum rounded, posterior margin
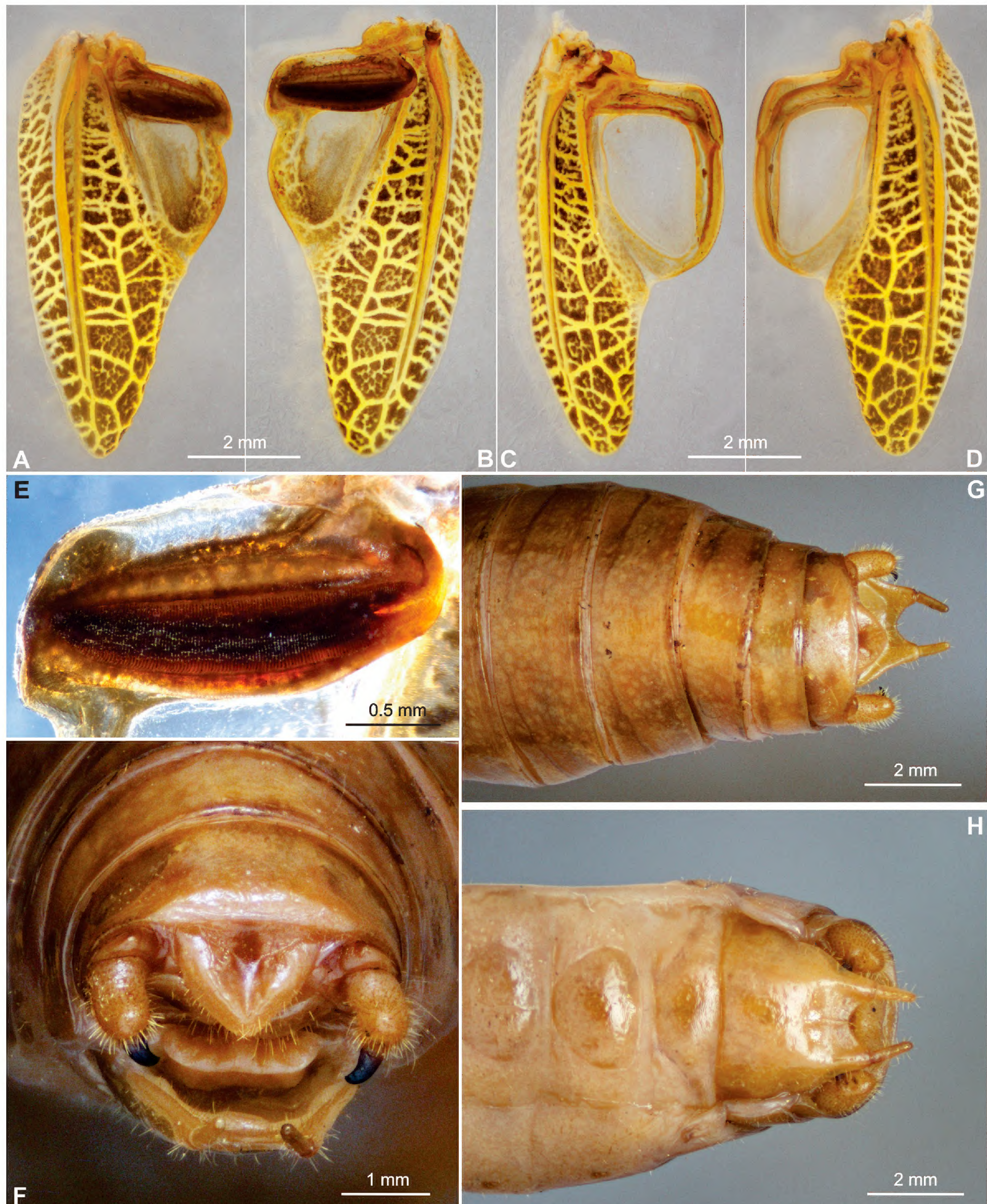

Fig. 2. *Dentotibium ramucantoris* **gen. nov. et sp. nov. Male. A.** Left tegmina in dorsal and **B.** ventral views. **C.** Right tegmina in ventral and **D.** dorsal views. **E.** Stridulation file. **F.** Male terminalia in axial, **G.** dorsal, and **H.** ventral views.

straight (Fig. 1B); pronotal disc slightly wavy in lateral view, rising between pro- and mesozone, descending at mesozonal sulcus, and rising again toward the posterior margin (Fig. 1D). *Wings.* Tegmina lanceolate, slimmed down toward the apex (Fig. 2A–D) and covering the third and fourth abdominal segments (Fig. 1A, B); tegminal M and R veins never converging, and Rs vein originateing near the tegminal apex (Fig. 2A); stridulatory file (=A1) almost straight, with 148–155 elongated and laterally flattened teeth (Fig. 2E), mirror of the left tegmina ovoid-shaped and two times as long as wide (Fig. 2C, D); tegminal A1 vein ventrally shaped as a fold with small, challenging-to-see denticulations (Fig. 1C). *Legs.* Forefemur ventrally armed with only a tiny spine on the inner margin close to the apex; foretibia armed dorsally with four tubercles on each dorsal margin; ventrally armed with seven spines on inner margin and two to four spines on outer margin. Mid-femur with two spines on the ventral-outer margin (Fig. 1D); mid tibia slightly dilated dorsally on first half, ventrally armed with five outer spines and two inner ones. Hind femur with three to seven spines on the outer ventral margin (Fig. 1A); hind tibia dorsally with four spine-like tubercles on the outer margin, and inner margin armed with nine or ten spines (Fig. 1B); internal genicular lobes of fore and middle femora armed, the rest without spines. *Abdomen.* Posterior margin of the tenth tergite straight (Fig. 2F, G); epiproct triangular, with rounded posterior border, lateral margins sub-elevate (Fig. 2F). Cerci tumescent, with a rounded apex and a preapical hook-shaped ventral spine curved downwards and toward the inner apex, strongly sclerotized and with a softly acuminated apex (Fig. 2F). Paraprocts wide, ovoid, unmodified; the subgenital plate quadrangular and almost as wide as long, with a pair of cylindrical styli in the distal margin and a moderately deep U-shaped notch between them (Fig. 2H). **Male genitalia.** Posterior margin of **lw.vl.** wavy; **up.vl** reduced in dorsal view, composed of two folds (one at each side) of medium length and grooved surface; **dl** short, with rounded posterior and lateral margins, without modifications or microstructures (Fig. 3A); **ti** softly golden colored, located in the posterior ventral surface of the genitalia, with no conspicuous modifications and with sparse holes along the surface (Fig. 3B, C); **ejd** tubular, progressively thinner toward inside the phallus, and with golden sparse microstructures on its medial region (Fig. 3A, B); **ejd** ending in the **vdl**, differentiated from the previously mentioned membranes (Fig. 3A) and looking like channeled conduct from axial vie; **ejv** rounded, middle-sized, and connecting with inner **ejd** of genital membranes (Fig. 3A, B).

Female. Similar to males in shape but notoriously larger; similar in color but with darker tones (Figs 4, 5). Tegmina covering up to the area between the fourth and fifth abdominal segments (Fig. 4A, B), epiproct similar to male's; conical and short cerci (Fig. 5D); ovipositor slightly curved upwards, dorsally wavy, without sawed, but ventrally with little saws over the last distal third, acuminate apex (Fig. 5E); ninth abdominal sternite quadrangular, with two inverted ear-shaped small prolongations over each end of the posterior margin and in between two lobes, covering the subgenital plate, the base with a depression, distal edge rounded and curving toward the external side and dorsal edge rounded and softly curving upwards (Fig. 5F, G); subgenital plate with a notch in the posterior edge, with every distal edge ending at an acute angle (Fig. 5G).

Distribution.—Mid and highlands of Boyacá, Colombia, between 1600 and 2300 m above sea level.
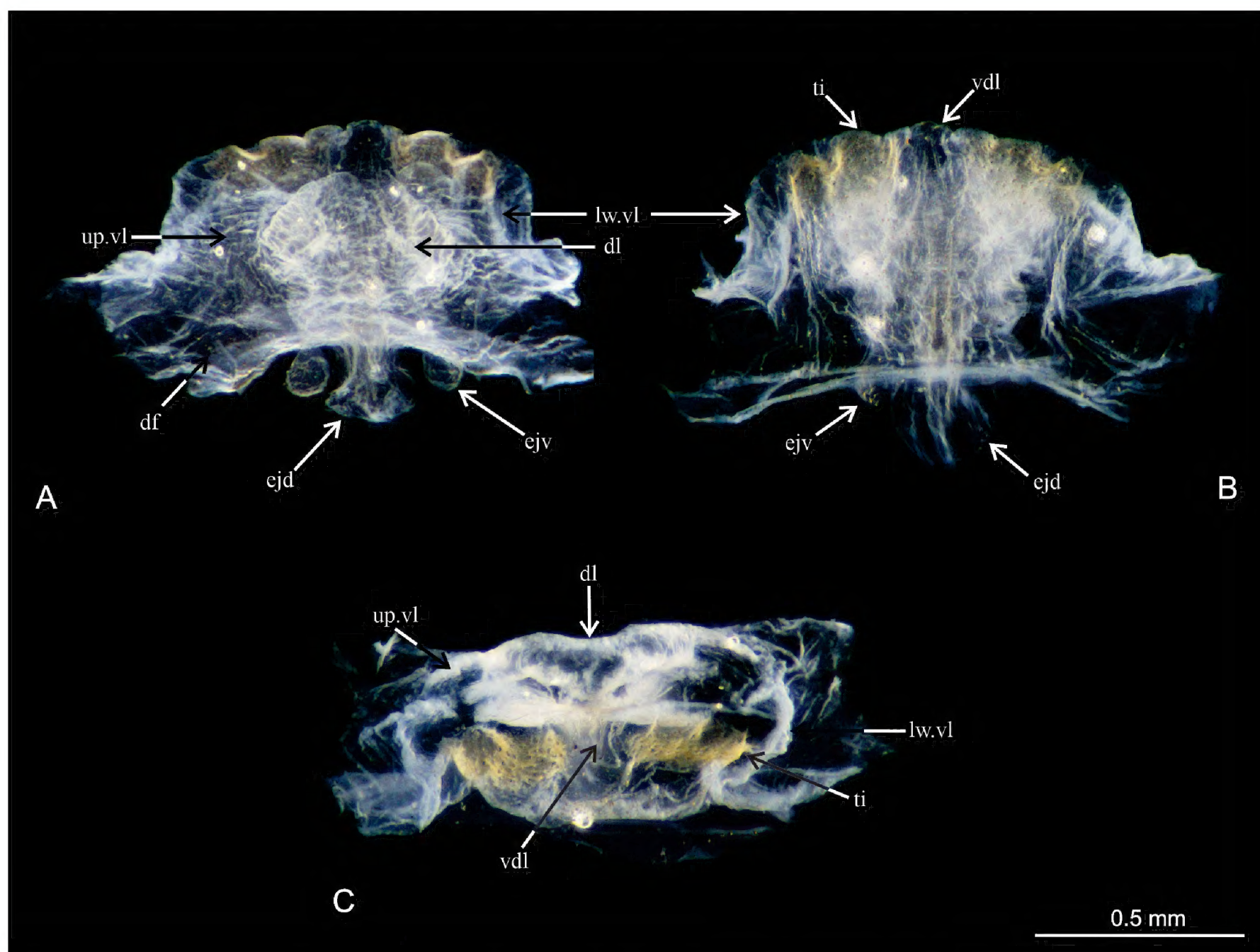

Fig. 3. *Dentotibium ramucantoris* **gen. nov. et sp. nov. Male genitalia. A.** Dorsal, **B.** ventral and **C.** axial views.

Table 1. Average pulse parameters of syllable sections of the calling song of *D. ramucantoris* **gen. nov. et sp. nov.** specimen B for 10 calls. ± standard deviation. The first three pulses per syllable of the introductory section and three randomly selected pulses from the middle selection were measured.

Section	Number of Pulses	Pulse Duration (ms)	Pulse Period (ms)	Pulse Peak Frequency (kHz)	Lower Bandwidth Limit (kHz)	Upper Bandwidth Limit (kHz)	Pulse Bandwidth (kHz)
Introductory	60	0.96 ± 0.14	3.27 ± 0.64	19.78 ± 0.63	17.40 ± 0.81	22.85 ± 1.12	5.45 ± 0.87
Middle	60	1.54 ± 0.39	2.95 ± 0.50	20.41 ± 0.56	17.50 ± 1.10	22.89 ± 0.41	5.39 ± 1.10

Variation.—The main variation present in the examined specimens is size: the ones from the midlands (Coper) are larger, having greater measurements than those from the highlands (Gachantiva). Midland females have black coloration in most of the medium and fore tibiae, while highland females' foretibiae are completely ochre.

Measurements.—(mm). **Male/Female: LB:** 21–30/34–36, **Pr:** 5–6/6–6.5, **Teg:** 8.5–9.5/16–17, **HF:** 10–11/15–16, **HT:** 9.5–10.5/15–15.5, **SP:** 2–3/2, **Ov:** 15–17.

DNA barcoding.—Baena-Bejarano et al. (2023) published the DNA barcoding sequence (Fig. 7) for the mitochondrial cytochrome c oxidase subunit I (COI) gene, (COI-5P) of the two paratypes here described under the same Operational Taxonomic Unit (OTU) and Barcode Index Number (BIN): BOLD:AEI5327 on the Barcode of Life Data System (Ratnasingham and Hebert 2007) [dx.doi.org/10.5883/BOLD:AEI5327].

Bioacoustics.—The calling song of *D. ramucantoris* **sp. nov.** consists of discrete syllables with a constant period of 485.60 ± 9.76 ms, duration of 73.52 ± 6.80 ms, and peak frequency of 20.46 ± 0.06 kHz (specimen B; Table 3) at 13.7°C and a 283.59 ± 8.39 ms period, 31.14 ± 2.60 ms and peak frequency of 20.36 ± 0.20 kHz at 21.6°C (specimen A; Table 5, Fig. 6). Each syllable corresponds to a complete opening and closing phase of the tegmina, as observed while recording the individuals. The syllable bandwidth decreases with increasing temperature, being 6.76 ± 0.28 kHz at 13.7°C and 3.97 ± 0.27 kHz at 21.6°C.

At the lower temperature (13.7°C) for specimen B recorded from 0.50 m, the syllable shows three differentiable sections (Table 2): the introductory section with three to four discrete pulses (Fig. 8E) of 0.96 ± 0.14 ms duration and a period of 3.27 ± 0.64 ms, the middle section with 1.54 ± 0.39 ms duration and 2.95 ± 0.50 period (Table 1) formed by complex wave pulses that seems to be the overlap of two simultaneous pulse trains (for which we measured the higher-ampli-

Fig. 4. *Dentotibium ramucantoris* **gen. nov. et sp. nov. Female. A.** Habitus in lateral and **B.** dorsal views.
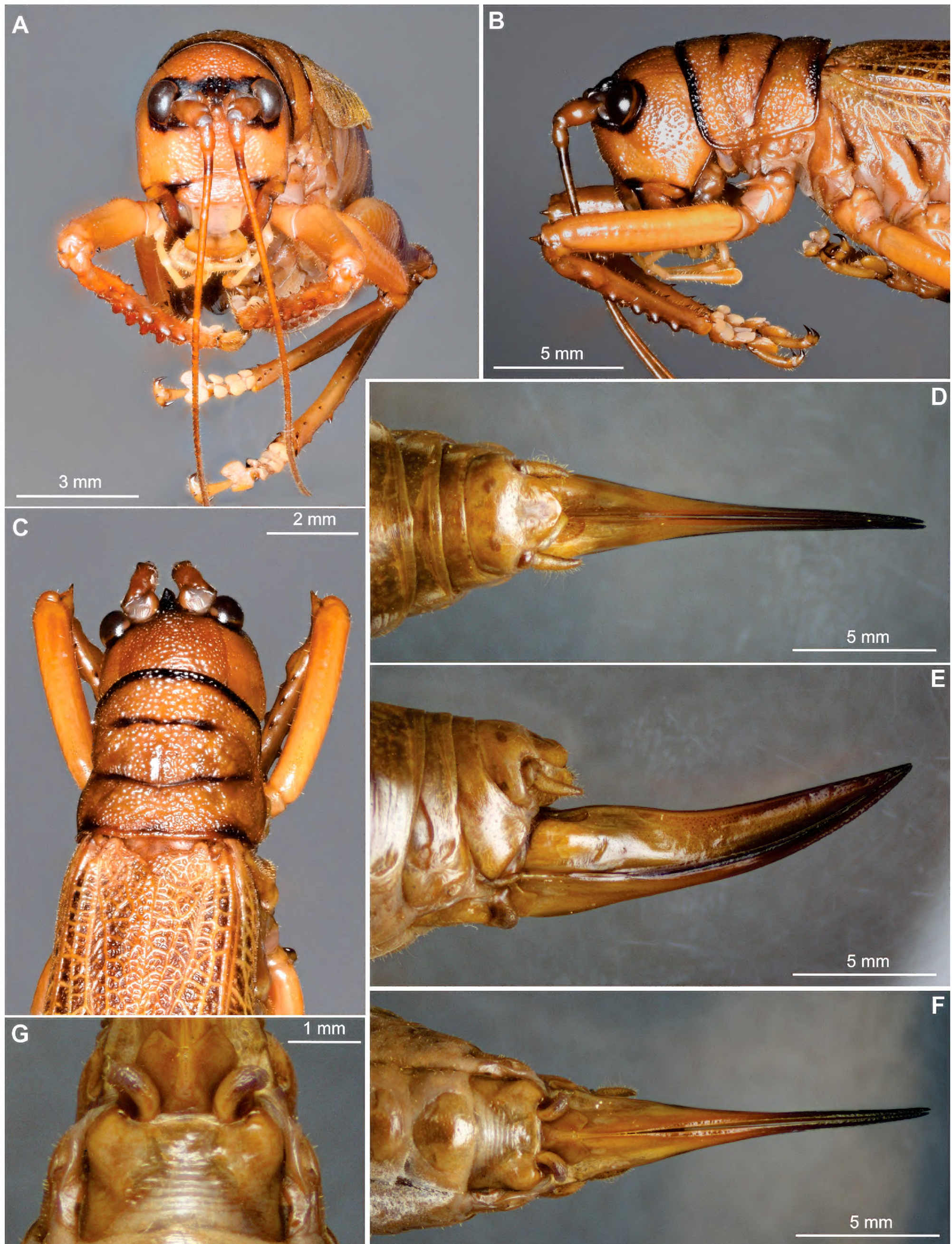
Fig. 5. *Dentotibium ramucantoris* **gen. nov. et sp. nov. Female. A.** Frons. **B.** Head and pronotum in lateral and **C.** dorsal views. **D.** Terminalia in dorsal, **E.** lateral, and **F.** ventral views. **G.** Subgenital plate.

Table 2. Syllable sections parameters of *D. ramucantoris* specimen B **gen. nov. et sp. nov.** for 10 calls ± standard deviation. The number of pulses for the final section was not measured due to difficulty identifying individual pulses.

Section	Number of Sections	# of Pulses	Section Duration (ms)	Section Peak Frequency (kHz)	Lower Bandwidth Limit (kHz)	Upper Bandwidth Limit (kHz)	Section Bandwidth (kHz)
Introductory	10	3.10 ± 0.32	10.15 ± 0.14	19.63 ± 0.10	17.16 ± 0.69	23.34 ± 0.81	6.18 ± 0.73
Middle	10	12.00 ± 1.25	38.97 ± 5.45	20.44 ± 0.11	16.55 ± 0.19	23.08 ± 0.11	6.53 ± 0.26
Final	10		16.07 ± 3.14	19.25 ± 1.36	15.50 ± 0.48	23.65 ± 0.40	8.16 ± 0.79

Table 3. Syllable parameters of *D. ramucantoris* specimen B **gen. nov. et sp. nov.** for 10 calls ± standard deviation. The number of pulses for the final section was not measured due to difficulty telling pulses apart.

Number of Syllables	Syllable Duration (ms)	Syllable Period (ms)	Syllable Peak Frequency (kHz)	Lower Bandwidth Limit (kHz)	Upper Bandwidth Limit (kHz)	Syllable Bandwidth (kHz)
20	73.52 ± 6.80	485.60 ± 9.76	20.46 ± 0.06	16.43 ± 0.13	23.19 ± 0.21	6.76 ± 0.28

Table 4. Syllable sections average pulse parameters of *D. ramucantoris* specimen A **gen. nov. et sp. nov.** for 10 calls ± standard deviation. The first ten pulses per syllable were measured. Recorded at 21.6°C and 50% relative humidity.

Number of Pulses	Pulse Duration (ms)	Pulse Period (ms)	Pulse Peak Frequency (kHz)	Lower Bandwidth Limit (kHz)	Upper Bandwidth Limit (kHz)	Pulse Bandwidth (kHz)
100	0.71 ± 0.10	3.18 ± 0.34	20.12 ± 0.40	17.56 ± 0.77	21.68 ± 0.34	4.12 ± 0.70

Table 5. Syllable parameters of *D. ramucantoris* specimen A **gen. nov. et sp. nov.** for 10 calls ± standard deviation. The number of pulses for the final section was not measured due to difficulty telling pulses apart.

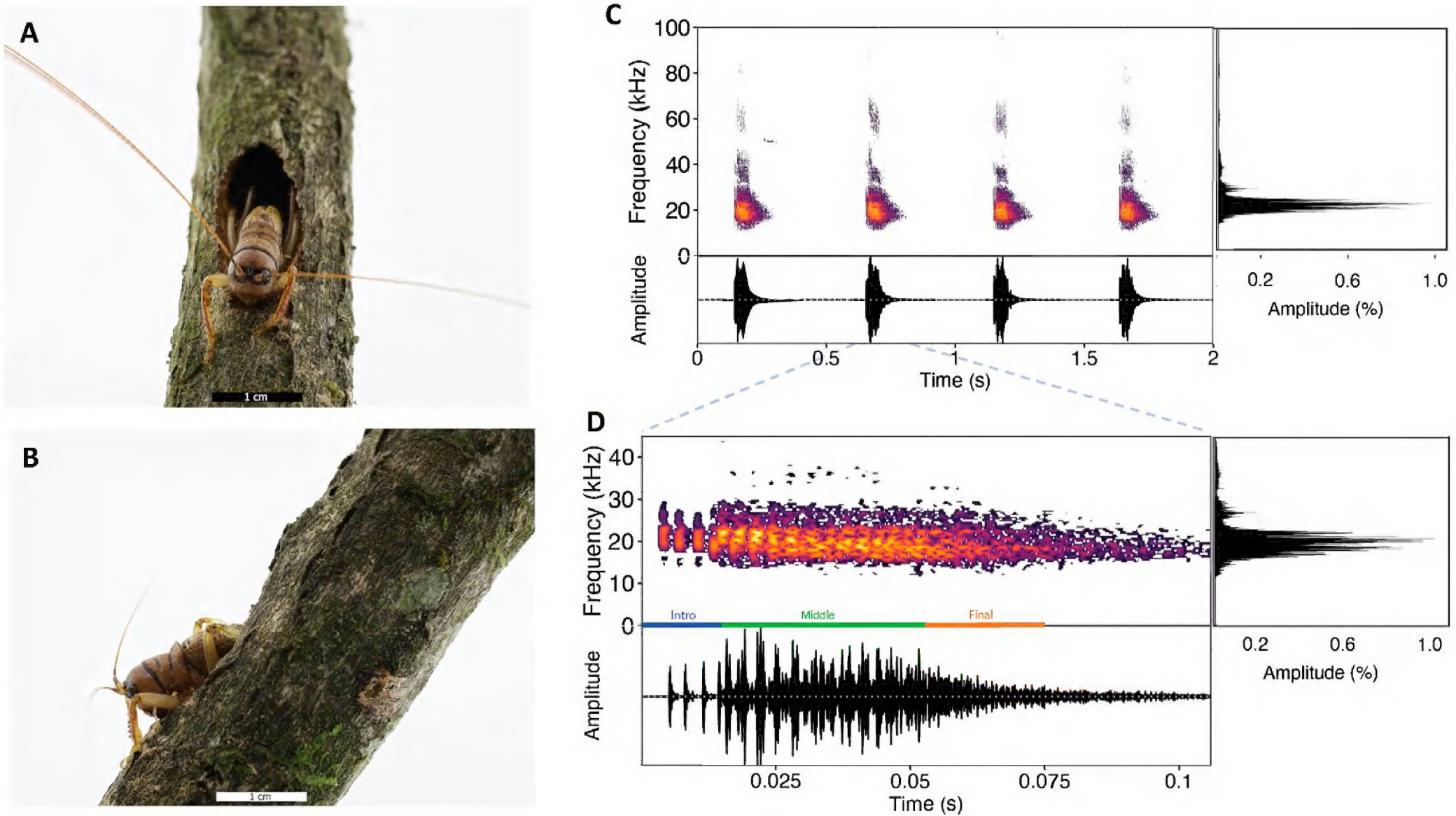| Number of Syllables	Pulses per Syllable	Syllable Duration (ms)	Syllable Period (ms)	Syllable Peak Frequency (kHz)	Lower Bandwidth Limit (kHz)	Upper Bandwidth Limit (kHz)	Syllable Bandwidth (kHz)
20	10.6 ± 0.68	31.14 ± 2.60	283.59 ± 8.39	20.36 ± 0.20	17.83 ± 0.30	21.81 ± 0.09	3.97 ± 0.27

Fig. 6. Photographs and calling song spectrograms of *Dentotibium ramucantoris* **gen. nov. et sp. nov. A.** Front view of a male in the burrow hole; **B.** Lateral view of the same male; **C.** and **D.** Spectrogram (top panel), oscillogram (bottom panel), and power spectrum (right) of four syllables (**C**) and one syllable (**D**) at different time and frequency scales (**D** has an amplitude threshold of -30 dB) for specimen B; 13.7°C and 85% relative humidity.

tude pulse train), and a final section of fading out amplitude with no distinguishable pulses of 16.07 ± 3.14 length (Table 1, Figs 6D, 8D).

For specimen A recorded at 21.6°C from 1.5 m, the syllable is made up of discrete pulses, of 0.71 ± 0.10 ms duration and with a 3.18 ± 0.34 ms period (Table 4; Fig. 8B). It also has an overlapping section, although the lower-amplitude pulse train is much more subtle (Fig. 8A).

The relationship between the overlapping pulse trains, temperature, and intraspecific variation requires further exploration. The syllable section units here described, as well as the -10 dB bandwidth lower limit and -10 dB bandwidth upper limit, might also be of importance to measuring intra- and interspecific variation.

Natural history.—Copulation behavior in *D. ramucantoris* **sp. nov.** occurs with males' and females' heads facing opposite directions usually inside the burrow in the lianas where they live, as was observed when we sliced the branches in two. The female presents the folds in the last abdominal sternite and subgenital plate (Fig. 5F, G), possibly to allow more efficient coupling. The territorial behavior of *D. ramucantoris* **sp. nov.** males is as follows: When a male gets closer to an occupied burrow, the dweller comes outside and raises their forelegs while opening their mandibles and emitting a defensive call. Unfortunately, we were unable to record the defensive call, and we did not observe any tremulatory or crepitating behavior.
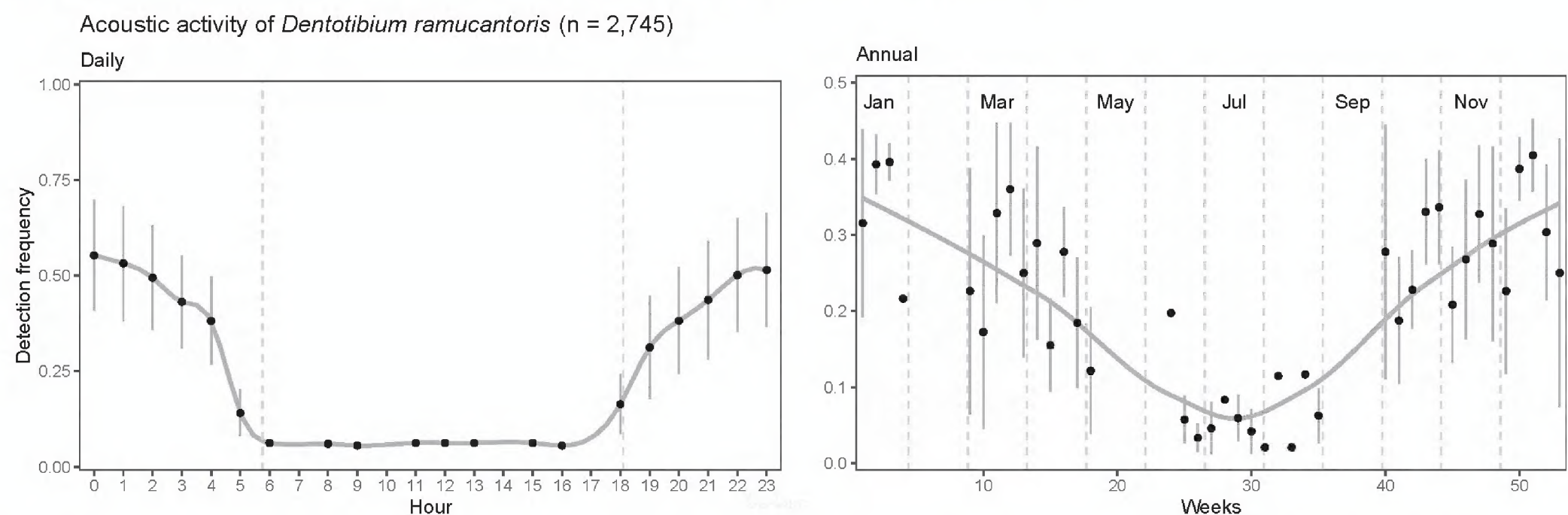

Fig. 7. Daily and annual acoustic activity of *Dentotibium ramucantoris* **gen. nov. et sp. nov.** from Reserva Natural y Cascada Los Tucanes in Boyacá, Colombia. The number in parenthesis is the number of recordings where the species was detected by the model (from a dataset of 11,882 recordings). Detection frequency was calculated as the number of recordings with a positive detection divided by the total number of recordings during the time period (hour and week). Dashed vertical lines represent the sunrise (05:46) and sunset (18:10) for the locality. Error bars represent standard deviation. Trend curves were calculated using locally estimated scatterplot smoothing.
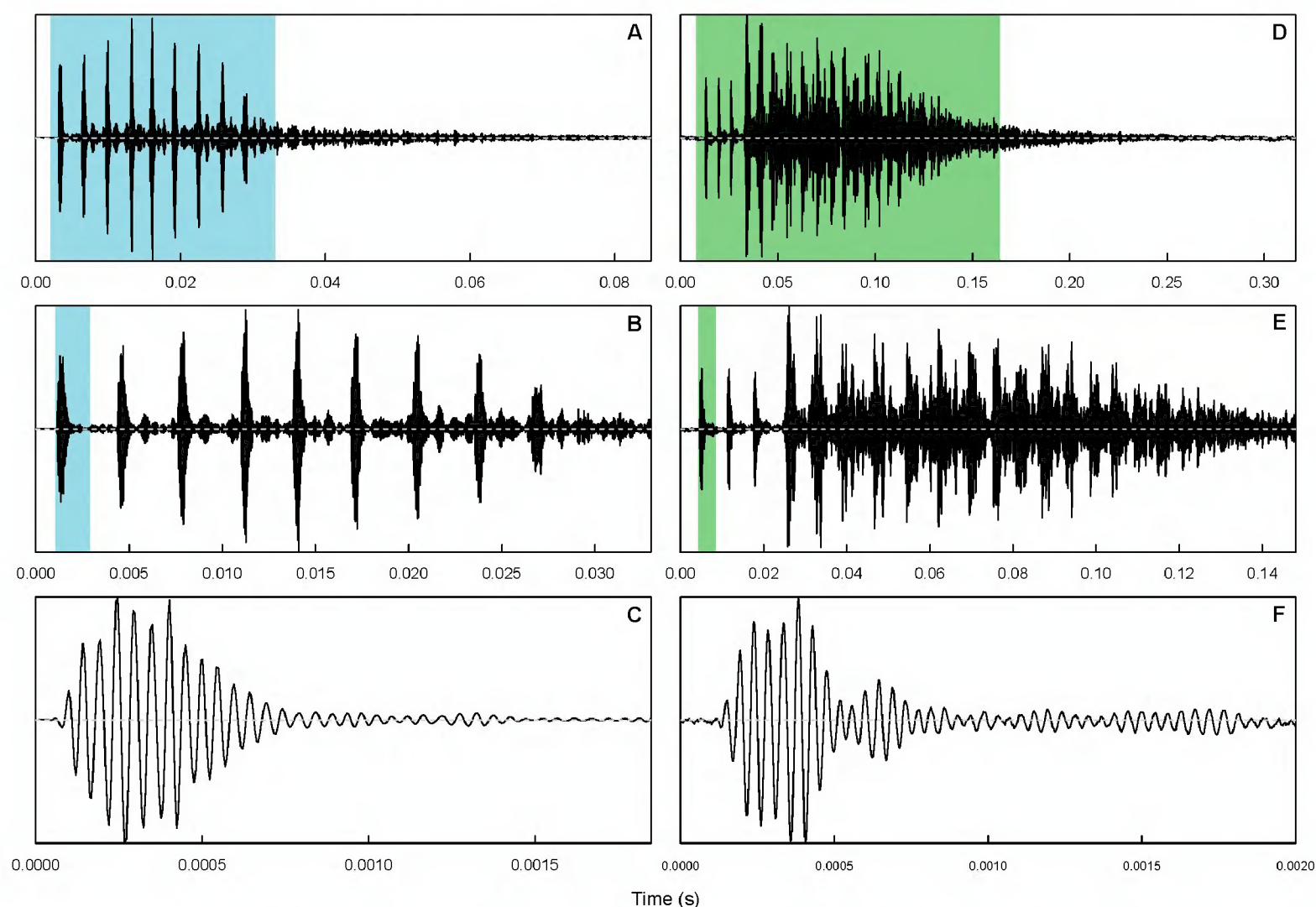

Fig. 8. Specimen A (21.6°C and 50% relative humidity) oscillograms of **A.** a syllable including the fading pulse train, **B.** close-up of the higher-amplitude pulse train section, and **C.** first pulse of the syllable. Specimen B (13.7°C and 85% relative humidity) oscillograms of **D.** a syllable including the fading pulse train, **E.** close-up of the higher-amplitude pulse train section, and **F.** first pulse of the syllable.

Males were seen singing from burrows on thin trunks, branches, or hard vines. Burrows were mostly located in the understory–midstory, but some were near the ground. The males were seen positioning the capital half of their body outside the entrance to sing [10.6084/m9.figshare.23257832], but they were also singing from inside after being disturbed. The burrow depth of other males' was variable, from ~20 cm to more than 35 cm. Future studies should seek a deeper understanding of how the burrows are made, and the remarkable natural history and ecological interactions of this new species.

Diel and annual singing schedule.—Based on the manual annotation of 1,306 recordings between March and May of 2020 from passive acoustic monitoring (Gomez-Morales and Acevedo-Charry 2022) complemented with the pattern matching model, males showed continuous acoustic activity from around 18:00 to 04:00 (Fig. 7), decreasing their activity before sunrise and ceasing acoustic activity during the day. Its calling song is conspicuous in the audible spectrum, can be heard from relatively long distances, and is easily distinguished. Gomez-Morales and Acevedo-Charry (2022) found a negative relationship between the acoustic activity of *Dentotibium ramucantoris* **sp. nov.** and the moonlight phase, a key environmental driver of its activity. We additionally identified the seasonal calling song patterns, finding a prominent peak of activity from October (week 40) to April (week 17) and then a decrease in activity mid-year (June–August; weeks 24–35) (Fig. 7), which matches the dry season of the study site (Secretaría de Salud de Boyacá 2013).

Discussion

Distribution patterns.—Regarding the distribution of the taxa closest to *D. ramucantoris* **sp. nov.**, *T. pilosula* is found on the eastern slope of the central Colombian mountain range and mainly inhabits cloud forests between 2000 and 2600 m. *G. sodalis* is found at medium altitudes between 1600 and 2000 m on the slopes of the inter-Andean valley of the Cauca River of the central and western mountain ranges. *N. foreli* is distributed in the inter-Andean valleys of the Cauca and Magdalena rivers of the three slopes or mountain ranges of the Colombian Andes, extending to the savannahs of the Caribbean region from sea level to 1000 m (Chamorro-Rengifo et al. 2011).

This contrasts markedly with the type localities, since *D. ramucantoris* **sp. nov.** would be the only related taxa discussed here found in the high Andean forests of the eastern Andean Mountain range between 1600 and 2300 m. There is considerable isolation between the distributions of the new species and both *T. pilosula* and *G. sodalis*; it is unlikely that the latter distributions are connected among themselves, as they are present on opposite sides of the central mountain range, the highest of the three Andean slopes that cross the country and can exceed 5000 m elevation. Furthermore, with the short wings and robust body of these three species, they are likely unable to fly and overcome the great heights of the central mountain range in order to cross the inter-Andean valley of the Magdalena River and then climb up to the high Andean forests of the eastern mountain range. This suggests that the morphology and behavior of these taxa may be convergent and subject to similar environmental pressures of the habitat. However, we encourage further research on Cocconotini biogeography and phylogeny to clarify the historic evolutionary relationship of the taxa.

Song, defense, and copulation from the branches.—The big heads found in ensiferans also exist in multiple genera and species. This characteristic is most remarkable in males and is usually related to territorial behavior (Judge and Bonanno 2008, Heller and Helb 2021). Such is the case for *D. ramucantoris* **sp. nov.**, where territorial behavior has been observed in which a burrow in the branch, used as an acoustic resonator, is defended by the male and occasionally by females. Such behavior could be an explanation for the big head present in females of the new species as opposed to other species with similar habits, such as *Gnathoclita*, where only the males have big heads, suggesting that females are not territorial (De Souza et al. 2011).

The signaling and copulation behaviors of *D. ramucantoris* **sp. nov.** may be associated with two factors: 1) the male dwelling in burrows on branches in lianas and 2) the small internal space of the burrow. Similar behaviors have been documented for field crickets and mole crickets, who dwell in underground burrows with little inner space and use them as acoustic resonators that allow for directional adjustment of their calling songs (Alexander and Otte 1967, Bennet-Clark 1970, 1998).

Copulation in *D. ramucantoris* **sp. nov.** happens inside the burrow with the head of the male and female facing opposite directions very similarly to mole crickets such as *Neocurtilla hexadactyla* (Perty, 1832) (Alexander and Otte 1967). However, *N. hexadactyla* has sclerotized genitalia (Cadena-Castañeda 2015), while *D. ramucantoris* **sp. nov.** lacks sclerotized components. This suggests that the male–female arrangement during copulation is likely a convergent result of the limited space inside the burrow rather than a result of morphological constraints.

The effect of burrow cavity characteristics on the calling song properties of *D. ramucantoris* **sp. nov.** has yet to be analyzed. Defense, communication, and copulation behaviors may have appeared convergently in different groups of katydids and crickets in response to similar lifestyles, most of which have yet to be documented.

Bioacoustics.—The discrete pulse period for specimen B (3.27 ± 0.64 ms at 13.7°C) is not significantly different from that of specimen A (3.18 ± 0.34 at 21.6°C), as the standard deviation ranges overlap, differing from the common acceptance that katydids in general tend to increase calling song pulse period in response to temperature (Cusano et al. 2016). We recommend the measurement of more individuals' songs to further assess the temperature-pulse period relationship for this species, as the lack of differences here may have been masked by intraspecific variation. Specimen B's calling song shows three differentiable sections in the syllable, as opposed to only one in specimen A. Temperature might affect scraper speed, generating varying rates of tooth contact and, hence, resonance (Morris et al. 2016) in the middle and final sections of specimen B's calling song at low temperatures; however, this hypothesis has yet to be confirmed.

Species with similar morphology and behavior in terms of singing from lianas, such as *T. pilosula*, *Nastonotus foreli* Carl, 1921, *Gnathoclita sodalis* Brunner von Wattenwyl, 1895, and *D. ramucantoris* **sp. nov.**, typically have a similar arrangement of the stridulatory file teeth: flattened laterally, with a small separation between them and located ventrally on a thick stridulatory vein (=A1).

However, the calling song of *D. ramucantoris* **sp. nov.** differs considerably from that of *T. pilosula*, as the latter is composed of syllables of two pulses with a period of 27–55 ms, against the more than 10-pulse syllables with a pulse period of 3.18–3.27 ms from *D. ramucantoris* **sp. nov.** The latter's pulse duration of 0.71 ms is less than half the 1.6 ms of *T. pilosula* at 21°C. This suggests a difference in either or both stridulatory file teeth size and wing

speed during stridulation. In addition, the syllable peak frequency of 20.36–20.46 kHz in *D. ramucantoris* **sp. nov.** is higher than the 17 kHz of *T. pilosula* (Morris and Montealegre-Z 2001).

While the calling song of *G. sodalis* is more similar to *D. ramucantoris* **sp. nov.**, it has a slightly longer pulse duration of ~0.8 ms with a shorter pulse period of ~1.8 ms, arranged in syllables of more than 20 pulses. Likewise, the peak frequency of the calling song of *G. sodalis* is considerably lower at ~16 kHz (Montealegre-Z and Morris 1999).

N. foreli has the most similar calling song, with a reported peak frequency of 20.00 kHz, which is very close to that of *D. ramucantoris* **sp. nov.** at 20.36–20.46 kHz, and a syllable duration of 10 ms, about a third of that of *D. ramucantoris* **sp. nov.** *N. foreli* also shares a similar number of pulses per syllable of around 10, followed by a section of fading out amplitude just as in the calling song of *D. ramucantoris* **sp. nov.** (Baker et al. 2019). It is likely that intraspecific variation in the calling song of *D. ramucantoris* **sp. nov.** is high, just as with *N. foreli*. However, in the present study, it was not possible to compare individuals further because of the relatively high background noise in the automatic detection recordings from the field and the distance from the individuals during these recordings.

We encourage future research to dive deeper into the detailed wing stridulation movement patterns of this genus and species and to expand the bioacoustics description provided here with more individuals from other localities to account for wider intraspecific and geographical variations.

Seasonal, circadian, and predator-prey activity patterns.—D. ramucantoris **sp. nov.** has nocturnal habits. This species is more acoustically active on nights with less moonlight than on moonlit nights (see "Katydid 5" in Gomez-Morales and Acevedo-Charry 2022), which might suggest that being more visible is a deterrent to continued singing. This, in turn, suggests that, despite dwelling within a burrow, males could be prey to nocturnal predators, such as gleaning bats, who might rely on vision for at least part of their targeting (Lang et al. 2016, Symes et al. 2020), as *D. ramucantoris* **sp. nov.** exposes about half of their bodies when actively singing (Fig. 6A, B).

This species shows uninterrupted singing throughout the night (Fig. 7), which is fairly uncommon among neotropical katydids, which usually proactively sing sparsely as their high-frequency songs may make them prey of eavesdropping bats and other nocturnal predators (Geipel et al. 2020, Symes et al. 2020).

We observed a couple of attempts of individual bats actively flying toward the burrow, but no success in catching the katydids. This could mean that bats actively eavesdrop on the high-frequency calling song of *D. ramucantoris* **sp. nov.** As a continuous singer, the adaptation of *D. ramucantoris* **sp. nov.** to avoid nocturnal eavesdroppers might be reactive. Their long and sensitive antennae were consistently kept outside of the burrow (even when retreating), which may allow them to sense movements: We observed the insect stop singing and retreat into the burrow when there was human movement at a distance of 1 m or less. Nevertheless, their response to the movements of flying bats remains to be assessed.

It is also possible that *D. ramucantoris* **sp. nov.** is able to detect echolocation calls and stop singing as a response, similar to the observed behavior in other continuous night signalers such as *Cocconotus wheeleri* (Symes et al. 2020), which has very similar circadian patterns. The retreating behavior and continuous nocturnal singing pattern of *D. ramucantoris* **sp. nov.** also

suggest a two-step predator–prey dynamic in which the predator eavesdrops on the katydid call as a first measure and then catches the prey based on visual cues once the katydid has stopped singing due to proximity. Following such a hypothesis, nights with more moonlight might increase predators' success in the second step, resulting in selection for lower acoustic activity on brighter moon nights to compensate by decreasing success in the first step, a theory supported by findings from previous studies (Lang et al. 2016, Gomez-Morales and Acevedo-Charry 2022) making *D. ramucantoris* a lunar phobic singer. To confirm or discard the predator–prey interaction hypotheses, we recommend further experiments on movement and echolocation sensitivity for *D. ramucantoris* **sp. nov.** as a possible model of reactive defense to predators.

This new species presents a strong seasonal singing activity showing considerably fewer calling song detections from June to August (Fig. 7). This pattern, to a lesser extent, has also been observed in other tropical katydid species in Panama (Symes et al. 2022). There are different reasons for such a shift in calling activity, such as increased foraging by predators (e.g., Jones et al. 2014), response to relative water or resource scarcity, or less abundance of adult animals. We recommend describing this species' diet, life cycle, and predator–prey interactions to fully understand their seasonal calling activity.

This work represents a promising example of an integrative taxonomic description (Padial et al. 2010) of a species with added value for future studies in systematics, evolution, and behavior. The bioacoustic description and barcoding will be relevant for future monitoring and profiling of the species (Riede 2018). We encourage future research in those regards and integrative descriptions of new taxa in the neotropics as a foundation for such studies.

Contributions

Acknowledgments

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Supplementary material 1

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Data type: xlsx
Explanation note: Raw acoustic parameter measurements.
Link: https://doi.org/10.3897/jor.33.116137.suppl1